An Account of the Anatomy and Homology of the Adipose Lobe of the Pelvic Fin of the Salmon.

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With Plate 43 and 3 Text-figures.

CONTENTS.

I. Introductory.

During the past two years the Zoological Department in Manchester University has been in receipt of fresh salmon, mainly from the Wye, which have been sent for the purpose of age determination by means of scale-markings. In December last Professor Hickson called my attention to the presence of a fleshy lobe lying immediately above the pelvic fin of a large female specimen. As we did not then know whether this growth was normal, and, if normal, whether it was confined to female specimens, I undertook to investigate the question; the investigation has not only proved exceedingly interesting, but has opened up a wider scope of research than I had anticipated.

On consulting various books on fishes I found that the lobe was invariably figured in the best drawings of the salmon; in Day's 'British Fishes,' for instance, it can clearly be seen.[1] At the same time no reference to the occurrence of such a lobe could be found in any book which might be expected to throw light upon a structure of this nature. I made a dissection of the adipose lobe, and so found that it was supported at its base by a splint of bone; the posterior, or distal, extremity of this bone was united to, but not fused with, the outermost fin-ray. This splint of bone is depicted in a figure of the pelvic fin skeleton of the trout in Parker and Haswell's 'Text-book of Zoology,'[2] and it is there mentioned that "the adipose lobe of the pelvic fin is supported by a small scale-like bone." By treatment of sections of the lobe with osmic acid and with Sudan III, I was able to satisfy myself that a considerable amount of fat was present in the lobe; I further observed from my sections that the lobe was stiffened by a plate of hyaline substance which ran throughout its length. I was fortunate enough to obtain a series of young salmon ranging in age from one to five months; from these I prepared serial sections of the pelvic region, and was thereby enabled to observe the origin and growth of the adipose lobe. From these observations I have been able to demonstrate that this so-called "adipose lobe" is nothing more or less than an enlarged scale which has never pierced its connective-tissue pocket. That a scale is capable of becoming a fin-like structure is an additional support to Mr. Goodrich's hypothesis, namely, that the dermal fin-rays (lepidotrichia) are modified body-scales, if his lucid argument has not already gained general acceptance.

I further examined the condition of the pelvic fins of other Teleosteans; and my observations from illustrations and from actual specimens go to show that an enlarged scale in the

[1] See also fig. 1 herein.

[2] Ed. 2, vol. ii, fig. 864.

outer angle of the pelvic fin is a character which is common to a wide range of members of that class. This "accessory scale," if I may so term it, is particularly characteristic of the more primitive Teleosteans, and is almost invariably absent in highly specialised forms; it is often well developed in actively swimming forms, and absent, or much reduced, in forms which haunt the ground. Only in the genus Salmo, so far as I am aware, is the accessory scale converted into an adipose lobe, and only in this genus, and perhaps in Coregonus, has it any skeletal connection with the fin-rays of the pelvic fin.

The nature of the function which this adipose lobe serves is obscure, but it is possible that it may assist in facilitating the rapid movements for which this fish is noted. The subject will be treated more fully at the conclusion of this paper.

I wish to acknowledge my indebtedness to Miss P. C. Esdaile, M.Sc., for permission to remove the portions of the salmon (which had been supplied by J. A. Hutton, Esq., for work upon which she was engaged) which I required, also for furnishing me with various particulars as to the size, age, locality and condition of the several specimens. To Professor Lorrain Smith I am indebted for the use of apparatus in the Pathological Department, and for his ready assistance in determining the nature of the fat in the adipose fins. Finally, I am glad of this opportunity gratefully to acknowledge the kindness of Professor J. W. Spengel for granting me a table for work in his laboratory at Giessen, and for the use of apparatus and materials; also that of Professor J. Versluys for his friendly interest and for many illuminative suggestions.

Figs. 1 and 2 illustrating this work were prepared from photographs kindly undertaken respectively by Mr. J. T. Wadsworth, of the Zoological Department at Manchester University, and by Mr. A. W. Brown, of the Gatty Marine Laboratory at St. Andrews.

II. Details of the Anatomy of the Pelvic Fin and of its Adipose Lobe.

(1) Anatomy of the Pelvic Fin.

The anatomy and development of the pelvic fin of the salmon has been described in a paper by K. G. Harrison,[1] and, as it is desirable that the environment of the adipose lobe should first be realised, I give below Harrison's summary of the anatomy:

"Die Lage der Bauchflosse variirt bekanntlich sehr stark bei den verschiedenen Teleostiern. Sie kann hinter, direkt unter, oder vor der Brustflosse liegen und wird dementsprechend bauch-, brust-, oder Kehlständig genannt. Die erste dieser Lagen ist natürlich als die ursprüngliche anzusehen. Diese findet sich bei dem Lachs. Diese Flosse ist an der ventralen Seite des Körpers gelegen, sehr nahe zur Medianebene, und ganz ventral von der Rumpfmuskulatur. Die Muskeln der beiden Flossen werden zum grössten Theil nur durch ein dünnes Lager Fettgewebe von einander getrennt. Kopfwärts ragt zwischen sie auf eine gewisse Streche der M. rectus abdominis hinein.

"Die Flossenstrahlen sind am Körper in einer schrägen Linie befestigt. Die Basen beider Flossen convirgiren somit caudalwärts gegen die Mittellinie. Der grosste Theil des primären Skeletes der Flosse besteht vorzugsweise aus einem Knochen, der als Basale metapterygii bezeichnet wird. Derselbe ist dreieckig und nur theilweise verknöchert. Die caudale Seite des Dreiecks ist die Kürzeste; an ihm articuliren vermittelst kleiner Radien die Flossenstrahlen. Die Länge des Knochens übertrifft seine Breite um ein bedeutendes und er dehnt sich, wie auch die Muskeln, weit von der Basis der freien Flosse nach vorn aus.

"Die Ebenen, in denen diese Knochen auf den beiden Seiten des Körpers liegen, convergiren dorsalwärts. Daher

[1] Harrison, K. G., "Unpaar. u. Paar. Flossen. d. Teleostien," 'Arch. für Mikr. Anat.,' 1895, p. 530.

liegen die Mm. Adductores beinahe ganz dorsal zum Knochen eingebettet zwischen Hartgebilden und Muskeln des Rumpfes, während die Abductoren zum grössten Theil ventral vom Flossenskelet sich finden.

"Der M. abductor superficialis entspringt von der Fascie, welche den tiefliegenden bedeckt und zieht zu der Basis eines jeden Flossenstrahles. Er ist der kleinste von allen Flossenmuskeln.

"Der M. abductor profundus entspringt von der medianen Kante des Basale und befestigt sich an der Innenseite der ventralen Strahlenhälfte.

"Der M. adductor superficialis ist leicht in zwei Portionen trennbar. Ein laugfaseriger Theil entspringt von dem oralen Ende des Basale und inserirt an den vier anterolateralen Strahlen. Ein Kursfaseriger Theil ist mehr oder weniger deutlich in einzelne. Muskelbündel zerlegt, die von der Fascie der Körpermuskulatur entspringen und an der Basis der caudalen Strahlen inseriren. Der Verlauf der letzten caudal gelegenen Muskelbündel ist beinahe vertical.

"Der M. adductor profundus entspringt vorzugsweise von der medianen Kante des Basale und ist symmetrisch zum entsprechenden Bündel des Abductor profundus an der Innenseite der dorsalen Strahlenhälfte befestigt. Der Muskel übertrifft an Masse den oberflächlichen Adductor um ein Bedeutendes.

"Die Nerven der Flosse bilden einen Plexus und stammen von sechs Rückenmarksnerven ab."

My observations bear out in every respect the above account of the musculature of the pelvic fin of the salmon, and I will only add that, in adult specimens, the tendons fastened to the bases of the fin-rays are very distinct; forwards, however, the muscle sheets are quite continuous, excepting that of the adductor superficialis, which, as Harrison remarks, is divided longitudinally into two portions. There are normally nine fin-rays in each pelvic fin, and though most authors quote ten as a variation from the normal, I have not yet met with this condition.

In addition to the bony elements of the pelvic fin, namely the Basale metapterygii and the lepidotrichia (dermal fin-rays), which have been mentioned above, there are in addition three small nodules, the distal pterygiophores (see fig. 2, *Pt.*). The precise position of these nodules varies not only in different specimens, but in the right and left fins of the same specimen. The largest pterygiophore is placed invariably, so far as my observations go, between the dorsal and ventral halves of the ninth, or inner, fin-ray. The middle pterygiophore varies in position, but not infrequently occurs between the dorsal and ventral halves of the fourth fin-ray. The outer pterygiophore occurs between the dorsal and ventral halves of the third or second fin-ray. In one specimen the middle and outer pterygiophores were bound closely together and occupied the space between the third and second fin-rays. On warming each of these pterygiophores in turn in a weak solution of caustic potash, the inner was found to remain single, but the middle and outer split fairly readily each into two distinct nodules. That all these several portions are ossified is indicated by the fact that they effervesce when placed in dilute hydrochloric acid.

Having now in mind the position and essential points in the anatomy of the pelvic fin of the salmon we shall proceed to locate and to describe the structure, known as the adipose lobe, with which it forms an intimate connection.

(2) Anatomy of the Adipose Lobe.

The lobe (fig. 1) lies in the angle between the pelvic fin and the body-wall in a position dorsal to and abaxial from the first, or outermost, fin-ray. It presents a vertical triangular surface when the fish is viewed from the lateral aspect, the acute-angled apex of the triangle being directed posteriorly; at the proximal end its section is approximately in the form of an equilateral triangle, whose apex is directed inwards and is united to the body-wall of the fish; at the aboral end the lobe is free and plano-convex in section, the convex side is adaxial and simply represents the result of the gradual rounding-off of the angular adaxial surface which has been noted at the proximal end. The outer vertical surface is grey in colour and firm in texture; the two inner surfaces, namely the dorso-lateral which faces the body-wall, and the ventro-lateral which faces the upper surface of the outermost fin-ray, are white in colour and soft to the touch. When at rest, the two inner surfaces of the lobe are closely apposed to the surfaces of the fish which they respectively subtend; as a result of this the soft ventro-lateral surface is grooved in its posterior half owing to the pressure of the fin-skeleton.

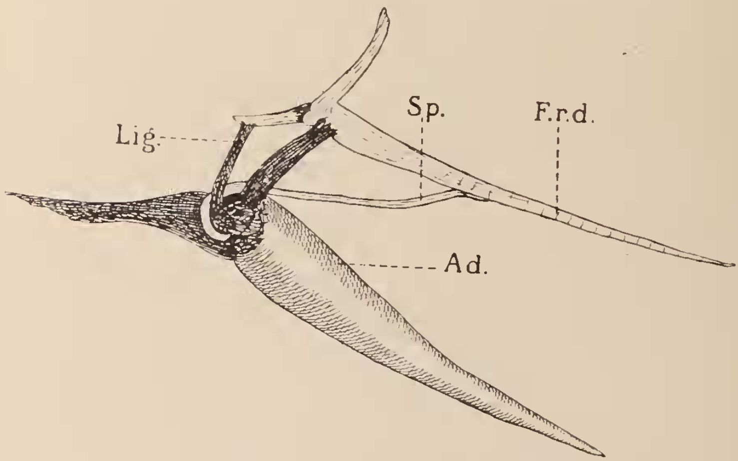
The lobe is equally well developed in specimens of both sexes, and, as far as one can judge from the comparatively few specimens which I have been able to examine, it further appears that the size of the lobe is not altered during the seasonal movements of the fish. Specimens were examined in the pink of condition, fresh from the sea, and others which had spawned and were, in some cases, infected with fungus, but neither the regular outline of the lobe nor its consistency appeared to differ in any degree; this is worthy of note, as it is well known that the body-scales of the salmon undergo a very marked disintegration at their margins, known as the spawning-mark, after the sexual products have been shed. Only in one unfortunate fish, which had long been suffering from an unsightly wound,[1] was the adipose lobe, on either side, reduced to a mere stump. The following measurements are from a male salmon weighing 22½ lb., 100 cm. in length, 52 cm. in girth, taken in the Wye, and will serve to convey an idea of the normal proportions of the adipose lobe:

Length of outer margin of pelvic fin .	10·0 cm.
,, inner ,, ,, . .	5·5 ,,
Breadth of distal ,, ,, . .	6·0 ,,
,, proximal ,, ,, . .	3·0 ,,
Length of adipose lobe	4·0 ,,
Breadth ,, (at base) . .	0·7 ,,

[1] A hole about an inch in diameter piercing the body-wall and entering the abdominal cavity in the anal region.

On removing the skin from the base of the adipose lobe and that covering the dorsal aspect of the outermost fin-ray a splint of bone, fig. 2 (*Sp.*), was observed connecting the fin-ray with the base of the adipose lobe. At its adaxial extremity this splint of bone is attached by connective tissue, just as two adjacent fin-rays are connected, to the dorsal half of the outermost fin-ray posterior to the point where the

TEXT-FIG. 1.



Adipose lobe from the left side to show its connection with the pelvic fin. The ligament connecting with the dorsal ramus of the head of the fin-ray has been severed, and the lobe deflected outwards through an angle of 180° (so that its inner, angular surface is presented). *Ad.* Adipose lobe. *F.r.d.* Dorsal half of the 1st fin-ray. *Lig.* Ligament. *Sp.* Splint of bone.

latter is joined by the ventral half; but while the two halves are still quite distinct, the splint in this region is rectilinear, and in girth somewhat more slender than the dorsal half of the fin-ray. At its abaxial extremity the splint curves sharply upwards so as to circumscribe the base of the adipose lobe (Text-fig. 1). There appear to be no muscles connected with the splint; it simply lies in a pocket of connective tissue, to the walls of which it is loosely attached; nor are there in the adult any muscles connected with the adipose lobe. On the inner aspect of the latter, however, near the proximal extremity, there are certain masses of tough ligament (*lig.*), which unite it with the heads of the dorsal halves of the first (outermost) and second fin-rays. Owing to this arrangement a certain amount of movement of the adipose lobe is consequent to the movement of the fin-rays, but there appears to be no mechanism for independent action. Further dissection of the lobe revealed the presence of an irregularly shaped mass of hard substance running throughout its length; near the base the mass is more or less spear-shaped, so that it appears linear in cross section; as the distal extremity is approached the section becomes triangular, but in all parts a flat surface runs parallel with, and close beneath, the vertical outer wall of the lobe.

(3) Histology of the Adipose Lobe.

Transverse sections, taken near the base of the lobe shortly before it loses all connection with the body-wall, are triangular in outline. Fig. 3 represents such a section together with the adjacent portion of the body-wall. The first feature of note is the entire absence of epidermis, not only on the surface of the lobe, but also on the surface of the opposing body-wall; this condition invariably obtained in the case of all adult specimens examined by me.[1] The lobe is bounded by a single strand of homogeneous material, which is slightly refringent and stains deeply with iron-hæmatoxylin; this strand I take to be the membrana basale (*M. b.*). Below the membrana basale the lobe is composed of dense connective tissue (*C. t.*), whose fibres run approximately

[1] It should be mentioned, however, that the fish had all travelled considerable distances before they reached me, so that the epidermis may have been rubbed off during transit or may have decomposed during the time that elapsed before the tissues were placed in the preserving fluid. I hope later to have an opportunity to clear this doubtful point by preserving carefully the adipose lobe from a salmon immediately it is taken from the water.

parallel to the surface of the lobe which they subtend. In the centre of the lobe there is a fatty tissue (*F. t.'*); the connective tissue here is loosely and irregularly arranged to allow space for the fat-globules. The latter have been dissolved by the action of alcohol in the preparation depicted in fig. 3; they will be described later when fig. 5 is examined. The accessory scale (*Sc. A.*), can be seen as a band of refringent substance running parallel to the vertical outer wall of the lobe throughout its entire height. It is surrounded by a scale pocket (*Sc. p.*). A normal body-scale (*Sc.*) is also shown in fig. 3; on comparing the accessory scale with this, it is seen that the former is very much the larger, but does not show the characteristic concentric markings. In thicker sections from this region of the lobe a few large pigment-cells were observed embedded deep in the outer vertical wall.

Fig. 4 represents a transverse section taken through the base of the adipose lobe quite close to its origin, where it is scarcely to be distinguished externally from the body-wall. Two scales (*S. c.*) are seen lying in their pockets (*Sc. p.*), close beneath the outer wall. The accessory scale (*Sc. a.*) is cut close to its root, and appears shorter and thicker than in the section shown in fig. 3; the arrangement of the tissues is similar in the two sections. Near the inner aspect a round space is seen (*Sp. h.*); this is due to the removal of the bony splint (Text-fig. 1, *Sp.*) which supports the adipose lobe. It was noticed above, under the description of the dissection of the lobe, that the splint lay in a pocket of connective tissue; now in the section, the hole (*Sp. h.*) is seen to be surrounded by concentric stands of connective tissue, which give it the appearance of a scale-pocket. This resemblance will receive further notice in the section on homology.

Proceeding towards the middle of the length of the lobe, where it is entirely free from the body-wall, we obtain a cross section which is still roughly triangular; such a section is shown in fig. 5. The outer vertical wall (*O.*), is approximately straight, the dorsal angle (*D.*) is acute, the ventral extremity (*V.*) has become flattened, the dorso-lateral border is markedly longer than the ventro-lateral, the latter is deeply furrowed. There is no epidermis; the outer border is, as before, formed by the membrana basale (*M. b.*) Immediately below the surface occur several layers of closely packed connective-tissue fibres. These run parallel to the surface which they subtend, and are very definitely defined; they are not shown in fig. 5, which was drawn from a hand-cut section; they appear, however, in fig. 6. There is a large accumulation of fat-globules (*Ft.*) in the central area; they appear as a band of orange running parallel with the accessory scale in sections stained with Sudan III. In addition a small clump appears in the central area on the outer side of the scale, where the latter makes a small bend away from the outer border of the lobe.

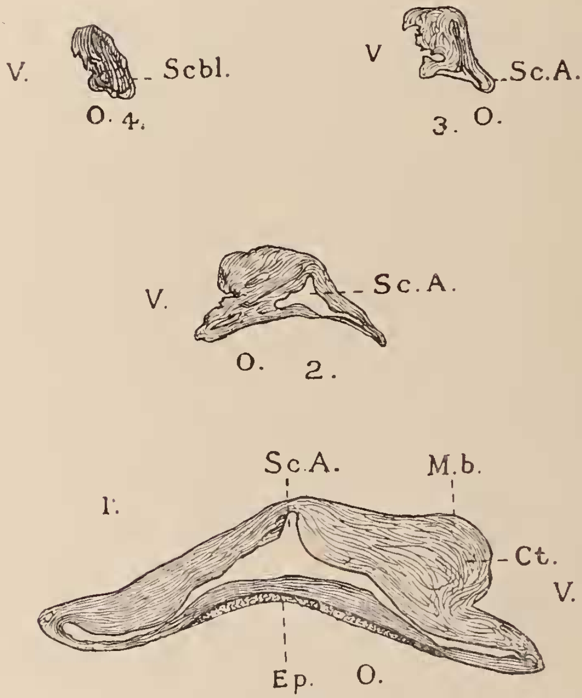
A few pigment-cells (*Pig.*) occur in the outer wall. The accessory scale (*Sc. a.*) is seen as a narrow strip of hyaline substance, running approximately parallel to the outer border of the lobe throughout the length of the latter. In sections from the same region of other salmon, there is sometimes a knotted swelling in that part of the accessory scale which lies within the broad portion of the lobe; it is more usual, however, to find this swelling nearer the distal end; such a condition is realised in fig. 6.

As the distal end is approached, the outline of the lobe and the shape of the accessory scale vary considerably in different salmon.[1] This is not surprising in an organ of such adventitious nature. The most constant and, moreover, the most striking feature of the distal area of the lobe is the presence of a patch of well-defined stratified epithelium. This epithelium, which is depicted in Text-fig. 2 (1), and under higher magnification in fig. 7 (*Ep.*), corresponds with the normal mucous epithelium of fishes; that is to say, it consists of round cells on the surface, passing into oval cells, and finally into palissade cells, the latter standing on a well-

[1] So far as I have observed they are always similar in both the adipose lobes of the same fish.

defined membrana basale (*M. b.*). Each cell contains a well-defined nucleus (*N.*). Serial sections show that this epithelium occupies an oval area a few millimetres from the tip of the lobe, and that it is confined to the outer vertical

TEXT-FIG. 2.



T. Ss. Adipose lobe of adult salmon. 1. In the region of the epidermis. 2. Slightly more than 3·5 mm. from the tip. 3. Slightly more than 1 mm. from the tip. 4. At the tip. *O.*, *V.* Outer, ventral aspects. *Ct.* Connective tissue. *Ep.* Epidermis. *M. b.* Membrana basale. *Sc. A.* Accessory scale. *Scbl.* Scleroblastic layer.

wall of the lobe. The invariable preservation of this epidermal tissue on a definite area, which is in no way specially protected, tends to suggest that the absence of epidermis from the remainder of the lobe is quite a normal condition. Beneath the membrane basale (*M. b.*) of the outer wall are numerous small pigment-cells (*Pig.*); a few large isolated pigment-cells occur deep in the dorso-lateral surface. The connective tissue (*C. t.*) is more open in texture than that of the proximal region; the elongated nuclei of the cells (*N.*) are clearly depicted; towards the surface the nuclei are fewer and rounder. The accessory scale in this region is typically triradiate in outline as appears in Text-fig. 2 (1), with a swelling where the rays meet; but it is sometimes compressed into masses, which are plate-like in section and much vacuolated. The succeeding sections sketched in Text-fig. 2 (2, 3) show that the scale is continued to the extreme distal end of the adipose lobe, though in the last, No. 4, it only consists of a layer of scleroblasts (*Scbl.*), by means of which growth is continued throughout life.

(4) Examination of the Fat of the Adipose Lobe.

Sections from all parts of the lobe, taken from fresh specimens or from those which have been preserved in 10 per cent. formalin or in Müller's fluid, give the characteristic blackening on treatment with dilute osmic acid. This treatment is not entirely satisfactory, for while the fat-globules turn black, the connective tissue is also affected to a certain degree, turning brown, and the fatty matter is not sufficiently clearly differentiated. A better result is obtained by treating hand-sections, or frozen sections, with Sudan III according to the method described by Lee[1]; the fat-globules are then stained a deep orange colour, while the other tissues are scarcely affected. The distribution of the fat in a section prepared in this manner is illustrated in fig. 5. Nearer the distal extremity the fat is almost entirely confined to the inner side of the accessory scale; towards the base it spreads to the outer side, where it occurs in very considerable quantities.

The fact that a stain is readily obtained with Sudan III at

[1] 'Microtomist's Vade-Mecum,' ed. vi, p. 376.

the ordinary room temperature indicates that the fat is in a liquid condition, as opposed to a fluid crystalline condition; for the staining is consequent upon the solution of the dye in the fat, and the solubility is greater in liquid fats than in fluid crystalline, while in crystalline fats it cannot occur (until they are melted). The fat-globules are only slightly refractile. These observations suggest that the fat is allied to olein, but it is unlikely that the deposit is composed of any one pure compound.

A further examination of the fat was made by staining with Kultschitzky's hæmatoxylin after mordanting with bichromate of potash. The significance of this method in relation to fats has been explained in a paper by Lorrain Smith and W. Mair as follows:[1]

"Weigert's bichromate hæmatoxylin method for the staining of myelin has become firmly established in histology. On studying the effect of the bichromate mordant on fatty tissue we were convinced that the myelin method could be extended to apply to ordinary fats such as occur in fatty liver and fatty myocardium. This proved to be the case, and we found that the points on which the method depends are the length of time during which the bichromating is carried on, the strength of the solution, and the temperature at which the solution is applied. We early discovered that positive results could be obtained with formalin sections of fatty liver and heart if these were mordanted in a bichromate solution kept saturated at 37° C. After a fortnight of this treatment sections of fatty liver or heart yield extremely well defined and sharp blue staining of the fat-globules with Kultschitzky's hæmatoxylin followed by differentiation in Weigert's borax ferricyanide solution. On investigating the chemistry of this reaction Dr. Thorpe found that the process is due in the first place to the oxidising action of the bichromate. In the process of oxidation of a molecule of fat the oxide of chromium (CrO_3) forms with it a compound which is practically insoluble in fat solvents. This

[1] "Fats and Lipoids in Relation to Methods of Staining," 'Skandinavischen Archiv für Physiologie,' 1911, p. 251.

compound in virtue of the chromium oxide which it contains is able to form a lake with hæmatoxylin. It is necessary, however, to distinguish two kinds of fat. The fats in which no unsaturated grouping occurs are not acted on by the bichromate solution. On the other hand, where the molecule of fat contains such a group there occurs a slow process of oxidation, and it is while this oxidation is going on that the insoluble fat-chrome compound is formed. The blue substance which then results from staining is a threefold body composed of fat, mordant, and dye. It becomes clear, therefore, that only the unsaturated fats can be stained by this process, and that on account of the ease with which they can be oxidised by the bichromate. We found also that the method may be applied to the staining of lipoid bodies in which unsaturated groupings occur such as cholesterin and cerebrosides.

"In the next place it is interesting to find that as the bichromating goes on and the fat becomes fully oxidised and saturated a stage is reached at which no staining takes place. It is only during the process of oxidation that the chromium oxide combines with the unsaturated molecule in such a way that it can lake the hæmatoxylin. Olein, for example, when oxidised by bichromate of potassium yields finally dioxystearic acid, and this fat will not stain by these methods."

A number of sections of the adipose lobe 5 mm. thick, from a ripe female fish taken in the Wye nets, were prepared on the freezing microtome. These were then placed in a saturated solution of potassium bichromate and kept at a temperature of 36° C. In order to observe the effect of oxidation induced by this treatment, sections were removed at intervals of twenty-four hours, and subjected to the hæmatoxylin (Kultschitzky) test as described above. For two days no coloration took place; on the third day two minute blue specks were observed, showing that oxidation had begun, and on each of the succeeding days up till the eighth very few blue specks appeared. On the ninth day the first obvious blue coloration was noted; the next day the specks were fewer, but darker in colour. This condition obtained till the nineteenth day, when the blue became more scarce again, indicating the approach of saturation. On the twentieth day, after which the observations were discontinued, the blue had almost disappeared.

A parallel series of observations was made with sections from the adipose dorsal fin of the same fish. In this case a distinct blue coloration was produced on the first day of bichromating, showing that oxidation had begun. The blue specks increased in number and in intensity of colour till the third day. The condition remained practically constant until the sixteenth day, when the colour became less intense and the specks fewer, indicating the approach of saturation. The fading continued until the twentieth, and last, day of the investigation.

While admitting that the foregoing experiments throw very little light, in the absence of other data, upon the chemical affinities of the fats under examination, they are highly relevant as emphasising the qualitative difference between them. We see, firstly, that the deposit in the adipose dorsal fin becomes oxidised much more readily than does that in the adipose lobe of the ventral fin; secondly, that the saturation point is approached at a correspondingly earlier date in the former than in the latter. We may, therefore, conclude that the fat in the lobe is of a more stable nature than that in the adipose dorsal fin.

III. The Development of the Adipose Lobe.

For the purpose of examining the details of the development of the adipose lobe I was fortunate enough to obtain a very complete series of young salmon, which were all hatched on the same day, and were removed from the water at intervals of a few weeks. The following table will show the age, size, and external appearance of the lobe in the eleven specimens which are to receive notice in this section :

No.	Age.	Length.*	Condition of adipose lobe.
1	5 weeks	23·5 mm.	No trace externally
2	6 ,,	25 ,,	,, ,,
3	7 ,,	24 ,,	,, ,,
4	8 ,,	24 ,,	,, ,,
5	10 ,,	24·5 ,,	,, ,,
6	12 ,,	26·5 ,,	,, ,,
7	14 ,,	27 ,,	,, ,,
8	16 ,,	29·5 ,,	,, ,,
9	19 ,,	34·5 ,,	Very slight papilla
10	21 ,,	41 ,,	Slight projection
11	23 ,,	43·5 ,,	Distinct lobe

* From tip of lips to fork of tail.

The specimens were fixed in Zenker's fluid. Transverse slices comprising the whole of the pelvic region were cut from each fish. These slices were embedded in paraffin, remaining in the oven for 1½ to 3½ hours, according to their size, and stained in hæmatoxylin (Grenacher[1]) on the slide.

(1) Description of the Sections.

In the youngest fishes examined (Nos. 1, 2 and 3) the splint makes its appearance in the series as an ossified strand, lying just beneath the surface in the upper angle of the fin-fold, and on a level with the plane which divides the two adductor muscles. Passing over a few sections in the posterior direction the head of the dorsal half of the first lepidotrich comes into view at the outer end of the basale and between the two adductor muscles; the splint in the same section is seen to be travelling ventralwards and outwards. Slightly beyond this again the splint is seen to come into close contact with the haft of the dorsal half of the first lepidotrich, so that the two together form a V-like structure of bone, lying in the dorsal region of the developing fin, with the angle of the V pointing towards the fin's proximal extremity. In the section last described the basale is still quite entire, and there is

[1] 'Practical Zoology,' Marshall and Hurst, ed. vi, p. 466.

not yet a trace of any of the other lepidotrichia, dorsal or ventral, in the region where the splint appears. This constitutes a marked difference from the condition in the adult fish, in which the junction of the splint with the dorsal half of the first lepidotrich occurs in the free portion of the fin outside the body-wall, and on a level with other lepidotrichia.

In No. 4 the splint is decidedly larger than in the foregoing specimens, and it is more curved. It first appears as a crescentic ossification placed nearly in the position noted above, but slightly higher up, for it subtends the adductor superior muscle. Further back, in addition to the portion which goes to meet the first lepidotrich, the upper extremity of the splint still remains in section as a disc of ossified tissue. No. 5 very nearly resembles No. 4, but in it the ventral half of the first lepidotrich appears in several sections before the splint finally disappears, a condition which is probably due to the greater extension of the fin (and consequently of the lepidotrichia) prior to sectioning, for it is not observed in the older and presumably more advanced specimens. In No. 5 is begun, and in Nos. 6 and 7 is continued, the blunting and obliteration of the primary fin-fold, which was so clearly defined in the younger specimens.

The body-scales are first clearly visible in No. 6. From No. 7 onwards there is an aggregation of connective tissue which forms a triangular area immediately above the fin; the base of the triangle is formed by the body-wall, and its acute apex points towards the division between the two adductor muscles. In No. 8 an abnormally large body-scale is found embedded in this triangular area, and this eventually becomes the accessory scale, the skeleton of the adipose lobe. In No. 9 the accessory scale is seen deeply embedded in the connective tissue of the body-wall at its basal anterior end; at the distal end it has grown towards the surface, and, pushing the body-wall before it, has formed a slight projecting papilla. The scale does not extend to the tip of the papilla.

The aggregation of connective tissue in which the accessory scale is embedded does not at this period reach the splint of bone which in the adult forms the support of the adipose lobe, which seems to indicate that the final condition is secondary. Not until No. 10 does the papilla lose connection with the body-wall on its inner aspect and become a free lobe.

In No. 11 the adipose lobe, though still relatively small, in outward appearance resembles the adult condition, only its outline is curved rather than angular. Vertical longitudinal sections of this specimen were prepared, and such a section containing the adipose lobe is depicted in fig. 8. The adipose lobe (*Ad.*) is seen lying in the angle between the body-wall and the ventral (pelvic) fin (*V. F.*). The epidermis (*Ep.*) has been very considerably damaged, but a trace of it still remains. A number of body-scales (*Sc.*) are seen, cut in various planes; they have not yet broken through their scale-pockets (*Sc. p.*) The accessory scale (*Sc. A.*) is cut somewhat obliquely, and is seen deeply embedded in the tissue of the adipose lobe; at this period it is scarcely distinguishable structurally from the normal body-scales, for it displays the characteristic thickened ridges, though in a much less marked degree. It is considerably longer than any of the normal body-scales; this does not appear in the drawing, but can easily be observed by following its course through the serial sections. Its proximal extremity, too, is much more deeply seated than that of the normal scales.

(2) Summary of the Development and Mode of Growth.

In the course of development the formation of the bony splint, which connects the first fin-ray with the base of the adipose lobe occurs at the same time as that of the fin-rays —i. e. long before there is any trace of the body-scales. It is plainly visible in sections from Specimen 1 onwards. The body-scales do not appear till Specimen 6 is examined. Only in Specimen 8—that is to say, sixteen weeks after hatching—is there any trace of the differentiation of the accessory scale, and the adipose lobe is not visible externally until the nineteenth week.

A scale, which is developed in a thickened area of connective tissue immediately above the base of the pelvic fin, is seen rapidly to increase in length, thenceforward gradually to lose its ridged markings and to become homogeneous in structure. This process begins about sixteen weeks after the hatching of the fish. As this specialised scale elongates it pushes before it the overlying tissues. First a ridge is formed in a horizontal direction along the body-wall; when the posterior extremity of the ridge reaches the space between the ventral fin and the body-wall, it leaves the latter and forms a slight projecting papilla. The papilla is at first conical, but, as the scale continues to grow, its outer aspect tends to become flat, the dorsal and ventral borders become sharply angular owing to the pressure of the edges of the growing scale, and the tissues on the inner aspect become largely adipose, in consequence of which its marginal walls fall inwards into folds along the lines of least resistance. Thus we arrive at the triangular outline of the adipose lobe which has been described in the adult salmon.

IV. Observations from other Teleostei.

(1) From the examination of other Teleostean fishes, and, where this was not practicable, from illustrations of such, it soon becomes evident that the occurrence of an enlarged scale at the outer angle of the base of the pelvic fin is a wide-spread feature of the order.

(2) The scale is constant for a given species.

(3) The scale is rarely absent from the Malacopterygian fishes, which are beyond doubt primitive Teleosteans, and is more constant in the less specialised forms in other groups.

(4) The scale is seldom seen in connection with ventrals which are thoracic in position, and never, so far as I am aware, with those which have reached the jugular position.

(5) So far as present observations go, the development of the accessory scale into an adipose lobe, possessing a skeletal connection with the ventral fin, is confined to the genus Salmo.

(1) Range of Fishes in which Scale has been Figured.

The following list of fishes in which the accessory scale is present is by no means complete, but will serve to indicate the wide range of its occurrence. I have not stated the groups from which it is absent unless I have actually observed this.

Sub-order—Malacopterygii.

Family Elopidæ . .	Elops saurus. Ox. 387, J. & E. 178.
	Megalops atlanticus. J. & E. 177, Camb. 547.
Hyodontidæ .	Hyodon tergisus. J. & E. 180.
	H. selenops. J. & E. 181.
Albulidæ . .	Albula conorhynchus. Camb. 548.
Gonorhynchidæ	Gonorhynchus greyi. Ox. 395.
Clupeidæ . .	None observed without.
Salmonidæ . .	Present in all genera except Osmerus, Thaleichthys, Mallotus and Hypomesus, which Boulenger regards as together forming a natural group. In Salmo is enveloped in connective tissue and largely surrounded by fat.

Sub-order—Ostariophysi.

Characinidæ .	Hydrocyon goliath. Camb. 578.
Cyprinidæ . .	Carpiodes cyprinus. J. & E. 71.
	Cyprinus carpio. Ox. 376.
	Labeo falcifer. Camb. 583.

[1] The references to figures are as follows. J. & E.: Jordan and Evermann, 'Fishes of North and Middle America,' vol. iv (plates), plate number. Camb.: 'Cambridge Natural History—Fishes,' page number. Ox.: 'A Treatise on Zoology,' pt. 9, Oxford, page number.

Siluridæ . . Trachinocephalus myops. J. & E. 235.
Synodus fœtens. J. & E. 236.

Sub-order—Haplomi.

Scopelidæ . . Saurus undosquamis. Gunther[1] 42. relatively enormous.

Sub-order—Percesoces.

Atherinidæ . Atherina stipes. J. & E. 332, long. thin scale.
Kirtlandia vagrans. J. & E. 336, very small.
Atherinopsis calafornieusis. J. & E. 341, very small.
Mugilidæ . . Mugil cephalus. Ox. 420, J. & E. 343.
M. curema. J. & E. 344, more marked than in M. cephalus.
Chætomugil proboscideus. J. & E. 346.
Agonostomus monticola. J. & E. 347.
Joturus pichardi. J. & E. 348.
Polynemidæ . Polynema quadrifilis. Camb. 641.

Sub-order—Acanthopterygii (Division Perciformes[2]).

Berycidæ . . Beryx splendens. Camb. 655.
Serranidæ . . Centropomus undecimalis. J. & E. 476, indistinct.
Hoplopagrus guntheri. J. & E. 513.
Neomenis. J. & E., present in all the species figured.
Oxiurus chrysurus. J. & E. 520.
Rhomboplites aurorubeus. J. & E. 521.
Apsilus dentatus. J. & E. 522.
Verilus sordidus. J. & E. 515, very small.
Acropomatidæ . Xenocys jeisiæ. J. & E. 526, very small.

[1] 'The Study of Fishes.'

[2] The accessory scale is not figured in any other division of the Acanthopterygii.

	Xenichthys agassizii. J. & E. 527, very small.
Pristipomatidæ	Hæmulon. J. & E. 528–32, present in all species figured.
	Lythrulon opalescens. J. & E. 536.
	Anisotremus surinamensis. J. & E. 538, very small.
	A. bilineatus. J. & E. 539, very small.
	A. virginicus. J. & E. 540, more marked.
	Orthopristis chrysopterus. J. & E. 541, very small.
	Microlepidotus inornatus. J. & E. 542, very small.
Sparidæ . .	Scale present in all Sparidæ figured.
Mullidæ . .	Mullus auratus. J. & E. 360.
	Mulloides rathburni. J. & E. 361.
	Upeneus maculatus. J. & E. 362.
	Pagrus auratus. Camb. 665.
Gerridæ . .	Xystema cinereum. J. & E. 556.
	Gerres olisthostomus. J. & E. 557.
Cyphosidæ . .	Kyphosus sectatrix. J. & E. 559.
	Hermosillia azurea. J. & E. 559.
Sciænidæ . .	Cynoscion. J. & E. 561–3. Present in all figured, but small.
	Sagenichthys ancylodon. J. & E. 564, small.
	Bairdiella chrysura. J. & E. 566, very small.
	Umbrina sinaloæ. J. & E. 571, small.
	Menticirrhus americanus. J. & E. 572, small.
Pomacentridæ .	Dacyllus aruanus. Ox. 443.
	Microspathodon chrysurus. J. & E. 593.
	M. dorsalis. J. & E. 594.
Scaridæ . .	Sparisoma hoplomystax. J. & E. 611, very small.
	Scarus cuzamile. J. & E. 612, very small.

	Pseudoscarus guacamaia. J. & E. 617.
Chætodontidæ .	Chætodipterus faber. J. & E. 619, small.
	Chætodon nigrirostris. J. & E. 620, doubtful.

(2) Personal Observations.

Having noted the above-mentioned list of fishes in which the accessory scale is figured, I next proceeded to examine the actual nature of such a scale in various specimens of fish in the collection at Giessen.

The scale was first examined in fishes most nearly allied to the salmon, and the following observations were made :

(1) In all the species of Salmo the accessory scale is encased in an adipose lobe, and is connected at its base by a splint of bone with the outermost fin-ray of the pelvic fin.

(2) In other genera of the Salmonidæ[1] the accessory scale is well developed, but it is not enclosed in connective tissue.

(3) In other Malacopterygian fishes, especially in those which are adapted for active swimming, there is usually a marked accessory scale.

In Clupea harengus this scale is very elongated, moreover it is subtended along its inner margin by a strip of skin, so that it forms a hollow conical outgrowth from the body; there is no bony connection with the fin-rays. In Hyodon sp. (?) there is an elongated hollow scale, as in Clupea, but no trace of connective tissue.

Passing next to the Ostariophysi, various Cyprinids were eligible for examination. A well-marked accessory scale was found in Abramis blicca, A. vimba, Squalius cephalus, Cyprinus (Leuciscus) dolula, Luciscus rutilus, and Chondrostoma nasus; but in Barbus vulgaris, though distinct, it is very small.

[1] Except in Osmerus, and probably also in Thaleichthys, Mallotus and Hypomesus, but I have not had an opportunity to examine actual specimens of the last-named genera.

Some specimens of Mugil cephalus which had lain many years in spirit were the next that came to hand. In these a triangular patch of skin devoid of scales was found in the normal position of the accessory scale; there was no trace of a lobe.

A few genera of Acanthopterygian fishes in which the accessory scale has been figured were lastly examined. In these there was a small flap or thread of skin in the normal position, but the skin was entirely devoid of stiffening matter of any sort. Among the Mullidæ, Mullus barbatus and M. furmutetus showed such a condition; in the former, however, the thread of skin was very slender, and the latter was badly preserved, so that it was not possible to judge of its normal condition. Among the Sparidæ, Sargus unimaculatus shows a distinct flap of skin, but the occurrence of any projecting tissue is very doubtful in another species of Sargus (not identified), and the same must be said of Charax puntazzo. At all events there is in these forms a certain area at the outer angle of the ventral fin which is covered by skin, but is devoid of scales.

V. Homology and Function.

In the foregoing pages we have examined the structure and the development of the adipose lobe of the pelvic fin of the salmon, and have seen from both these points of view that it resembles a body-scale. We have further noted that the presence of an accessory scale, or, in some instances, of a flap of skin in a corresponding topographical position, is a widespread feature of Teleostean fishes. That the adipose lobe is morphologically neither more nor less than a large body-scale which has never broken through its surrounding pocket is too obvious to require proof, but it would not be right to leave such a remarkable structure with no more than a platitude of this kind. The possibility of deriving the dermal fin-rays from body-scales, through the intermediary of a fin-like scale, such as we have in Salmo, occurred to my mind before my attention was called to the admirable paper by Mr. Goodrich,[1] which deals with the same question from the developmental point of view. The following is a summary, in his own words, of Mr. Goodrich's observations:[2]

"Besides these body-scales are found scale-like exoskeletal elements set end to end in rows and forming jointed dermal fin-rays, called lepidotrichia, supporting the web of both the paired and the median fins. The minute structure of these fin-rays is almost or quite identical with that of the scales of the fish to which they belong. This is true more especially of the lower forms. In some, such as Amblypterus, there is a perfect gradation in form and arrangement between the body-scales and the fin-ray elements. But, as a rule, the transition is more abrupt, the segments of the rays acquiring a squarish or oblong shape, and not overlapping. Both the scales and the lepidothrichia are embedded in the dense connective tissue, the fibres of which enter the substance of the bone. Movable joints are formed by the fibrous matrix remaining unossified between them."

In the light of these facts, what had been but a passing idea acquired a real significance. The resemblance between a scale covered by connective tissue and a lepidotrich might easily be accounted for on grounds of analogy; but since we know that fin-rays are developed from scale-like elements, it seems just to regard the fin-like scale of Salmo as a connecting link between a body-scale and a lepidotrich.

The fin-like nature of the adipose lobe is enhanced by the fact that it is connected by a splint of bone with the ventral fin. What, then, is the homology of this bony splint? We have noted that in the course of development it appears together with the lepidotrichia, which it resembles in structure, at a period before there is any trace of body-scales. Its position in the adult fish (p. 710), see fig. 2, indicates that it represents the dorsal half of an additional lepidotrich. If

[1] Goodrich, E. S., "On the Dermal Fin-rays of Fishes," 'Quart. Journ. Micr. Sci.' (v), vol. 47, 1903.

[2] 'A Treatise on Zoology,' Oxford, pt. ix, p. 212.

this homology is true, it should be noted at the same time that the ventral ramus of the head is wanting, as is also all trace of a ventral half; moreover, while the lepidotrichia are characteristically jointed, the splint is composed of a single piece.[1] These points are apparent in Text-fig. 3. It was further observed that the splint lies in a pocket of connective tissue, which in section resembles a scale pocket (see fig. 4, *Sp. h.*). The resemblance does not necessarily prove the homology of the two structures; it is merely satisfactory as not dispelling the idea. Taking the sum of these considerations we must suppose that we have to deal with the head

Text-fig. 3.

The first (outermost) lepidotrich of the pelvic fin, together with the splint of bone which supports the adipose lobe, seen from the inner aspect. *Sp.* Bony splint (probably = dorsal half of a tenth lepidotrich). *H. d.* Head of dorsal half of first lepidotrich, with its dorsal ramus *d.*, and ventral ramus *v.* *H. v.* Head of ventral half of 1st lepidotrich.

and dorsal ramus of an additional lepidotrich which exhibits certain scale-like properties. Whether this lepidotrich is in the process of development or whether it is the vestige of a once fully developed ray I cannot at present decide with certainty, but its secondary fusion tends to show that it is vestigial. The exact homology of the adipose lobe itself is more obscure; that it arises as a scale we have seen. It is unlikely that it ever functioned as a fin-ray, or part of a fin-

[1] This is not necessarily a dissimilarity, for it will be noticed that the heads of the lepidotrichia are also devoid of joints, and the splint is only equal in size to the head of a fully developed Lepidotrich. The unjointed condition of the heads of the Lepidotrichia is, without doubt, due to secondary fusion.

ray, for in that case it would have reversed its course of evolution to a quite unimaginable extent. It is equally unlikely that it is a rudimentary fin-ray, or part of a fin-ray, since it contains but one large scale (instead of a series set end to end), and further, it lies dorsal to all parts of the fin skeleton. It is alienated from any fundamental resemblance with the adipose dorsal fin, in the first place because it develops comparatively late in the life of the fish, it is an adventitious outgrowth, that is to say, not the result of the development of a pre-existing embryonic fold (as is the case with the adipose dorsal) ; in the second place its fatty matter is of a different composition, and it is devoid of horny rays (actinotrichia). It seems probable, then, that the adipose lobe of the pelvic fin of Salmo is an organ sui generis. This does not detract, however, from its importance as suggesting the lines by which a fin may have been derived from a scaly outgrowth of the body-wall.

The function of this remarkable structure presents a puzzle to the investigator. It is almost impossible to believe that an organ of such large dimensions and regular occurrence in the genus Salmo serves no useful purpose in the daily round of these fishes. It seems justifiable to dismiss summarily the idea that it is a storage organ ; the relatively stable properties of its fatty matter, the development of a stiffening axis, and its invariability in salmon of varying physical condition all point in this direction.[1] Again, as it is equally developed in both sexes, it is probably not analogous with the "claspers" of Elasmobranchs. Günther has laid stress on the value of the paired fins of fishes as balancing organs.[2] The pectorals and pelvics are placed where they are required to support the greatest weight of the fish on which they occur ; thus the salmon, being thickly built in the posterior abdominal region, requires large ventrals. The adipose lobes may then act as additional balancing organs for the pelvic region ; further, situated as they are just in the outer angle of the pelvic fin

[1] Except in one extreme case, see p. 709.

[2] 'The Study of Fishes,' p. 44.

(see fig. 1), they may act as dams to prevent the back-wash of water, which would be considerable in a fish with large pelvics, and so facilitate the swift motion through the water for which the salmon is noted.

EXPLANATION OF PLATE 43,

Illustrating Mr. Edward W. Shann's paper, "An Account of the Anatomy and Homology of the Adipose Lobe of the Pelvic Fin of the Salmon."

Lettering.

Ad. Adipose lobe. *B. m.* Basale metapterygii. *C. t.* Connective tissue. *Cu.* Cutis. *Ep.* Epidermis. *F. r. d.* Dorsal half of a fin-ray. *F. r. v.* Ventral half of a fin-ray. *Ft.* Fat-globules. *Ft.'* Fatty tissue from which the fat has been extracted with alcohol. *M.* Muscle. *M. b.* Membrana basale. *N.* Nuclei. *Pig.* Pigment-cells. *Pt.* Pterygiophores. *Sc.* Body-scale. *Sc. a.* Accessory scale. *Sc. p.* Scale pocket. *Sp.* Splint of bone which supports the adipose lobe. *Sp. h.* Hole caused by the removal of the splint of bone which supports the adipose lobe. *V. f.* Ventral (pelvic) fin. *O., D., V.* Outer, dorsal, and ventral aspects.

Fig. 1.—A portion of the right side of a Wye salmon showing the pelvic fin; a piece of black pasteboard has been placed beneath the adipose lobe to render its outline more distinct. Photograph by Mr. J. T. Wadsworth, Manchester. $\times \frac{2}{3}$.

Fig. 2.—Skeleton of the right pelvic fin of a Wye salmon, seen from the ventral aspect; the rays are spread out and separated from the Basale metapterygii, with which in the natural condition they closely articulate. The numbers refer to the lepidotrichia. Photograph by Mr. A. W. Brown, St. Andrews. Slightly reduced.

Fig. 3.—Transverse section of the adipose lobe, abou tone third of the length from the basal end, together with the adjacent body-wall. From a Rhine salmon, whose adipose lobe measured 35 mm. by 6 mm. The sections, of which this is one, were block-stained iron-hæmatoxylin, and cut 30 μ thickness.

Fig. 4.—Transverse section of the adipose lobe at the base (the lobe is quite continuous with the body-wall). Rhine salmon, dimensions not known. Method of preparation as above.

Fig. 5.—Transverse section of the adipose lobe in the middle region, to show the distribution of fat. ♀ fish from the Dovey; recently spawned, 18 or 19 lb., 35¼ in. by 17¼ in.; shape very like a "fresh" fish. Not at all emaciated; no fat on the pyloric cæca; five years old. Hand section, stained Sudan III. × 18.

Fig. 6.—Transverse section of the adipose lobe slightly distalwards from the middle. ♀ fish from the Wye, 29¾ in. by 15 in.; full of ripe eggs. No sign of emaciation; no fat on the pyloric cæca. Stained hæmatoxylin, cut 16 μ in thickness.

Fig. 7.—Transverse section of the outer wall of the adipose lobe near its distal end, to show epidermal epithelium. ♀ fish from the Wye, 35 in. by 19¼ in.; spring fish, unspawned. Great accumulation of fat on the pyloric cæca; nearly five years old. Prepared as above.

Fig. 8.—Vertical longitudinal section of the pelvic region of a young salmon. Age of fish twenty-three weeks; length, 43·5 mm. Stained hæmatoxylin, cut 12 μ in thickness.